

On the Structure and Occurrence of Maxillulæ in the Orders of Insects.
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(PLATE 31, and 17 Text-figures.)

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INTRODUCTION.

A QUARTER of a century ago Hansen (1893) originated the theory that the pair of appendages associated with the hypopharynx of *Machilis* and other Apterygota is homologous with the maxillulæ of Crustacea (21)*. The theory has since been raised to the status of an established fact, chiefly by the embryological researches of Folsom. In the paper in which his results are recorded, Folsom (17. p. 116) stated that "The superlinguæ (maxillulæ) should hereafter be recognised as morphologically important structures, and be searched for in even the most specialised haustellate orders"

Since this forecast was made its value has been proved by re-researches on the constitution of the hypopharynx in Coleoptera and Lepidoptera. In the larvæ of certain genera of these orders the presence of structures of undoubtedly maxillular nature has been demonstrated.

The present paper is a record of investigations whose object has been to determine as far as possible the occurrence of structures comparable with maxillulæ in the various orders of insects. In the haustellate orders only the mandibulate larvæ are considered. The Hemiptera, Mecaptera, and Thysanoptera are not dealt with. Some attempt is made to compare the form of maxillulæ characteristic of different orders and, where enough material has been available, to study the distribution and variation of these structures within the order.

I wish to express my gratitude to Professor S. J. Hickson, F.R.S., who

* My attention has recently been called to the fact that Lubbeck in his monograph of the Thysanura and Collembola recognises the maxillulæ as appendicular structures, referring to them as "a second pair of maxillæ."

has kindly allowed me to work in the Entomological Laboratory of the University of Manchester.

I find it impossible to express how greatly I am indebted to Dr. A. D. Imms for the invaluable assistance he has rendered in innumerable ways. To him I owe the suggestion of the subject of investigation. I am glad to have this opportunity of thanking Dr. Imms for the immense amount of trouble he has taken in the furtherance of this work.

Terminology.—Folsom in 1899 furnishes a complete list of the various terms employed up to that date to designate the hypopharynx and maxillulæ. To these latter terms, proposed by Hansen, he objects on the grounds that they imply unproved homology. He proposed to call the median element of the compound "hypopharynx" the "lingua," and its lateral appendages the "superlinguæ." His objection to Hansen's terms can no longer hold after his own proof of the correctness of the assumption of this homology.

Investigators on the morphology of the mouth-floor in Eudopterygota speak of the median portion as the hypopharynx and the lateral lobes projecting from or situated upon it as maxillulæ. These terms possess the advantage that they are free from the possibility of confusion with others used to designate portions of the labium. They will for these reasons be employed in the present paper.

APTERYGOTA.

Machilidæ.—The maxillulæ are figured by Oudemans (35) under the name "Paraglossæ." They are described in some detail by Hansen (21, p. 31). They are, he says, independent of the hypopharynx near the base of which they are articulated to the skeleton of the head. He notes the "small single jointed palp," and observes that each appendage shows, towards the tip, a tendency to cleavage into two lobes. A detailed figure is given by Carpenter (6). He refers to the "spicules, ridges and pits" which occur on their surface, and states that the outer lobe of each is articulated with the basal sclerite. They have, he says, "all the appearance of a reduced pair of jaws."

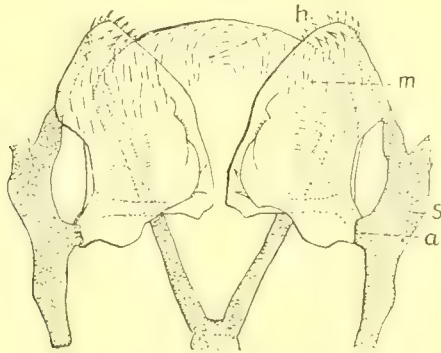
Petrobius sp.—*P. oudemansi*, Carpenter (?). The headless remains of the specimens were kindly identified as far as possible by Professor G. H. Carpenter. Since these appendages are in *Machilidæ* in a less rudimentary condition than in any of the other insects considered in this paper, their structure in this species has been studied with some care. Observations made on simple dissections were supplemented by examination of preparations treated with potassic hydrate, and others, which in addition were stained with acid fuchsin.

The maxillulæ, which lie between the mandibles and first maxillæ, are seen, after the removal of these pairs of jaws, to stand on the floor of the mouth, above the base of the hypopharynx. Of this organ they obscure all but the

extreme tip. Pl. 31 is drawn from a preparation in which the maxillulæ were pressed apart so as to expose the hypopharynx. This latter measures $\cdot 56$ mm. in length. The length of the left maxillula is $\cdot 59$ mm. and its greatest width $1\cdot 9$ mm. A pair of long peduncles (*p.e.*) support the hypopharynx.

The cavity of the maxillula was found to be undivided; the sutures separating the lobes consisting of no more than ridges and grooves in the upper wall only. Of these ridges, that which marks off the outer lobe, arises beyond the palp. At its base is the rounded, chitinous structure (*a.*) suggestive of an articulation. A short distance behind the apex of the inner lobe there projects from the depression between this and the outer lobe the curious structure (*h.*), armed with six curved teeth, which point towards the surface of the maxillula; the portion of the palp (*p.*) beyond the lateral wall measures $\cdot 14$ mm. in length.

Text-fig. 1.



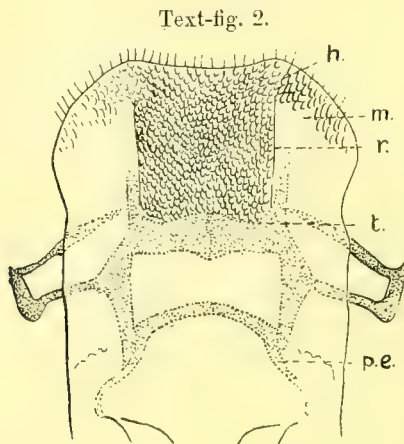
Campodea lubbocki. Dorsal aspect. From a preparation stained with acid-fuchsin. Pressure has been applied and the maxillulæ are displaced outwards. $\times 250$.
a. Articulation of maxillula. *h.* Hypopharynx. *m.* Maxillula. *s.* Supporting skeleton.

Campodeæ.—In his paper on the *Campodeæ*, Meinert (32) described the lingua and paraglossæ of *Japyx* and of *Campodea*. The lingua, he says, is small in the former genus and the paraglossæ large and bilobate. In the latter the appendages are large and flat, entirely covering the dorsal surface of the oval lingua. Hansen (21) states that the two genera are closely allied as regards the structure of the mouth-parts. He agrees with St. Traunfels that in *Japyx* the maxillulæ consist of an inner lobe, an outer lobe, and a three-jointed palpus. In dealing with these structures, in *Lepidocampa fimbriatipes* Carpenter (8) states his belief that this outer lobe and palpus were rightly referred to the maxillæ by Börner in 1908.

Specimens of *Campodea lubbocki* (Silvestri) (for the identification of which I am indebted to Mr. R. S. Bagnall) were collected at Fallowfield, Manchester.

The structure of the hypopharynx and maxillulæ is illustrated in text-fig. 1. The hypopharynx measures $\cdot 09$ mm. in length and $\cdot 12$ mm. in greatest breadth. In its natural condition it is almost obscured by the maxillulæ (*m.*), which are articulated at (*a.*) to a short branch of the skeletal support (*s.*). They are laminar, and can be removed entirely from the hypopharynx. The distal portion is triangular and the pointed apex furnished with sharp teeth directed inwards. The dorsal surface is covered with setæ, those of the anterior and inner areas being borne by scales arranged in rows. Each maxillula measures $\cdot 11$ mm. in length and $\cdot 05$ in total width.

Lepismidae.—Hansen (21) states that in the structure of the hypopharynx *Lepisma* stands between *Machilis* and the Orthoptera. His statement is referred to by Carpenter (8. p. 13), who described the tongue of *Isolepisma* and the maxillulæ borne by it. These latter have "a roughened apex, with



Lepisma saccharina. Dorsal aspect of tongue. *h.* Hypopharynx. *m.* Its maxillular surface. *p.e.* Peduncles. *r.* Longitudinal ridge marking inner edge of maxillula. *t.* Anterior transverse bar of skeletal system.

fine short bristles," and there is "no differentiation into lacinia and galea." The tongue of *Lepisma saccharina* (text-fig. 2) is a broad membranous structure closely applied to the surface of the labium. It is supported distally by a system of sclerites, composed of elements corresponding to those of *Isolepisma*. The width at the base is $\cdot 2$ mm. and the distance from the transverse bar (*t.*) to the anterior edge $\cdot 12$ mm. The maxillulæ have become completely fused with the tongue, of the upper surface of which they form the lateral portions, being separated from the median scaly portion by longitudinal ridges (*r.*).

Collembola.—Maxillulæ appear to be present in all Collembola as a pair of delicate lamellæ intimately associated with the hypopharynx. A frequently

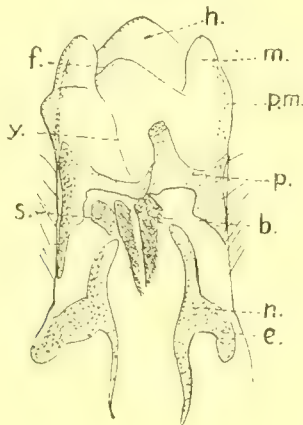
occurring feature is the presence of a fringe of tooth-like projections or of setæ along the inner margin.

Isotoma palustris was regarded by Carpenter (6) as possibly one of the least specialised Collembola. He described at the apex of the maxillula an indication of cleavage into two lobes. Of the Achorutidæ *Anurida maritima* is the subject of Folsom's well-known work of 1900. Reference has already been made to his conclusions with regard to the nature of the superlinguæ. An exact account of their structure is to be found in the Monograph of Imms (24).

DERMAPTERA.

Forficula.—In his paper on *Hemimerus talpoides*, Hansen (22) devotes considerable attention to the hypopharynx and maxillulæ which he describes and figures in detail (pp. 70, 71, fig. 10). I have also been able to examine the hypopharynx of specimens of *Hemimerus hansenii*, Sharp, kindly determined by Professor Carpenter and collected by Dr. J. W. S. Macfie at

Text-fig. 3.



Forficula auricularia. Dorsal aspect of tongue. $\times 80$. *b.* Brush-like sclerite. *f.* Asymmetrical fold in dorsal wall of hypopharynx. *h.* Hypopharynx. *m.* Maxillula. *n.* Chitinous plate in inferior wall of pharynx. *p.* Transverse skeletal bar. *p.m.* Chitinous rod in outer wall of maxillula. *s.* Small sclerite.

Accra, Gold Coast. I found it essentially similar to that of *Forficula*. The main differences concern the degree of fusion of the maxillulæ with the hypopharynx, and the details of construction of the transverse elements of the skeletal support.

We find in *Forficula* a roughly oblong tongue (text-fig. 3) lying above the labium. It is produced distally into a median (*h.*) and two lateral (*m.*) membranous lobes, corresponding to the hypopharynx and maxillulæ respectively

of *Hemimerus*, although each is considerably shorter in proportion to its width than are the corresponding organs in this latter genus. In one adult specimen they measured .02 mm. in length and their width at the base was .02 mm. The hypopharynx extended beyond the level of their bases to a distance of .03 mm. and its greatest breadth was .07.

Proximally the floor of the mouth bears the pair of asymmetrical sclerites (*n.*) from the side of which the plates (*e.*) extend downwards to be closely associated, at their ventral extremities, with the inner angle of the mandible. These sclerites have an exact counterpart in *H. hanseni*, Sharp, although in the latter case there is no sign of asymmetry. Anteriorly we find in *Forficula* a chitinous arch consisting of two asymmetrical sclerites (*p.*), the small piece (*s.*), and the curious setiferous median sclerites (*b.*), which will be referred to when we come to consider the Psocidæ and Mallophaga. In this position in *H. hanseni*, Sharp, however, we find only a single slender arch of chitin immediately above which the maxillulæ arise.

In all the specimens examined the dorsal wall at the base of the hypopharynx exhibited a tendency to form the curved fold (*f.*) whose apex lay considerably to the left of the median line. A similar fold at the base of the left maxillula gave this organ a bilobed appearance.

The ventral surface of the tongue is stiffened by a continuous plate of yellow chitin. This plate extends forwards to a short distance behind the base of the hypopharynx. It is associated at its anterior lateral corners with a slender chitinous rod (*p.m.*) which supports the external wall of the maxillula. In this position I found a more plate-like sclerite in *H. hanseni*, Sharp.

It is probable that *Forficula* is derived from a form in which the hypopharynx and its lateral appendages originated as far back as the transverse sclerite. Such a condition would resemble more closely that of *Hemimerus*. This supposition is supported by the presence of a faintly marked suture (*y.*) extending back from the inner angle of the left maxillula to this skeletal bar.

ORTHOPTERA.

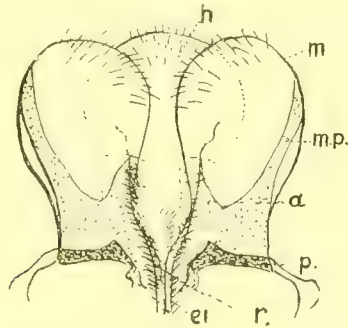
Folsom (17. p. 115) gives an account of the hypopharynx of Orthoptera. The lingua he says "corresponds exactly with the lingua of Apterygota." He finds that the chitinous supporting stalks described by Miall and Denny are comparable to those in Apterygota. In *Melanopus femoratus*, Folsom discovered "superlinguæ" as "large dorso-lateral rounded lobes intimately united with the lingua." He notes the evidence of the presence of lingua and superlinguæ in Packard's figure of *Anabrus*, Packard (36). The tongue of Blattidæ is described by Mangan (29. p. 3, pl. i. fig. 1). "The free tip," he says, "is furnished at the sides with a pair of elongate plates (*Z*) which

carry bristles, and are continuous behind, as thin rods, round the opening of the salivary duct; . . . The position of . . . (Z) is conformable with the idea that they may represent a pair of maxillulæ." Schimmer (39) describes the hypopharynx of the Gryllid *Myrmecophila*. On the ventral surface are borne a pair of elliptical plates covered with fine setæ. Mjoberg (34) has no hesitation in homologising these plates with the so-called "lingual glands" associated with the hypopharynx of Psocidæ. The nature of these latter structures will be discussed below, but here it may be remarked that Enderlein (15) regards them as maxillulæ.

EPHEMERIDÆ.

As the well-known figure of the lingua and superlinguæ of *Heptagenia* Vayssière (45) makes evident, these structures attain a very well-developed condition in the Ephemeridæ. No attempt had at that time been made to homologise the lateral appendages with maxillulæ. Vayssière was, however,

Text-fig. 4.



Chloëon dipterum. Tongue of nymph. $\times 90$. *a*. Articulation of maxillula. *h*. Hypopharynx. *m*. Maxillula. *m.p.* Plate in ventral wall of maxillula. *p.* Transverse sclerite at base of maxillula. *r, ei*. Setose ridges at base of hypopharynx.

so much impressed by their appendicular appearance that he proposed to regard the Ephemeridæ as insects provided with a secondary labium, consisting of the median "langue" together with its "deux appendices." Eaton, in his monograph of 1883, figures the "tongue" and "paraglossæ" of the nymphs of a large number of Ephemeridæ. Though the latter organs show considerable variation in size relative to the former, they are never wholly absent. Hansen (21) refers to them as maxillulæ. This view of their nature is supported by the figure of the head of a young larva of *Ephemeræ*, in which Heymons (23. Taf. ii. fig. 29) clearly shows that they are originally distinct from the hypopharynx. From his description (p. 22) it is evident that Heymons regards the appendages as lateral portions of the hypopharynx.

Folsom (17. p. 116) is convinced of their homology with the lingua and superlinguæ of *Anurida*, which in a certain stage of their development bear a great resemblance to Heymons' figure of *Ephemera*.

Chloëon dipterum.—The oval hypopharynx (text-fig. 4) measures ·3 mm. in length and ·21 mm. in breadth at the widest part. The maxillulæ (*m.*) resemble this structure in shape and size, and in the membranous nature of their walls. Each measures ·2 mm. in width and extends ·3 mm. beyond the sclerite (*p.*). Each maxillula is supported ventrally by a curved chitinous plate (*m.p.*), which is proximally merged with the chitinised posterior portion of the wall of the hypopharynx.

The inner edges of the maxillulæ are continuous with a pair of convergent setose ridges (*r.*), which extend backward along the upper surface of the hypopharynx. Outside these occur a second pair of ridges (*ei.*) also bearing setæ, whose distal portions lie on the upper surface of each maxillula.

PERLARIA.

Packard (36) describes the hypopharynx of Perlidæ as "an unusually large tongue-like mass nearly filling the buccal cavity." I have examined this organ in the adult of a species of *Perlodes* closely resembling *P. dispar*, and find that it answers to the above description. No signs of maxillulæ were discovered.

The larvæ of the two sub-orders *Plecoptera filipalpia* and *Plecoptera setipalpia* Klapalek (27) are distinguished by the structure of the labium. This in the former group is apparently less specialised than in the latter. An examination of the hypopharynx in the two genera *Leuctra* and *Nemura* of the Filipalpia and *Perlodes*, *Chloroperla*, and *Perla* of the Setipalpia suggests that the form of this organ offers a further distinction*.

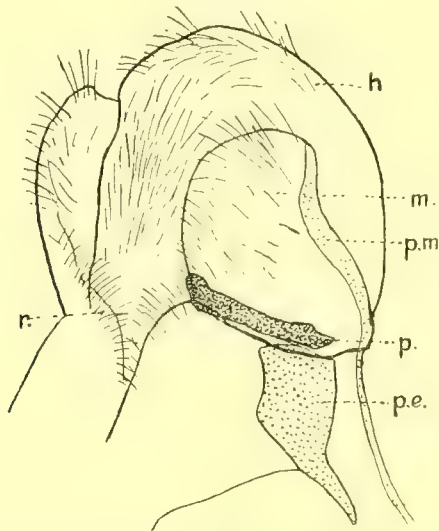
Nemura.—In the larva of an undetermined species of this genus the hypopharynx (text-fig. 5) is a much-rounded structure convex dorsally. The surface is thin and membranous. It measures ·13 mm. in length and ·2 mm. in width in a specimen with length of abdomen 2·88 mm. From its dorsal surface project two large lobes (*m.*) measuring ·09 mm. in length and ·05 mm. in width, which extend laterally some distance beyond the hypopharynx, and whose cavities are confluent with that of the latter. Ventrally a chitinous plate (*p.m.*) supports the free portion of each lobe. Proximally the dorsal surface of the hypopharynx (or ventral wall of the pharynx) bears a pair of setose ridges (*r.*). Each ridge is distally continuous with the inner margin of the lateral lobe. Thus the position of these ridges agrees strikingly with

* The only traces of maxillulæ associated with the large fleshy tongue of larval Setipalpia were a pair of very small setiferous lobes, but in the Filipalpia these organs were large, and well developed and similar in both genera examined.

that of a similar pair which have been described in *Chloëon*, if we regard the structures (*m.*) as the homologues of the maxillulæ of this Ephemeroïd. Further comparison gives additional grounds for this assumption. The lateral lobes are in both cases fused with the hypopharynx on its dorsal surface. They extend beyond it laterally. In both cases they are supported ventrally by a chitinous plate, and a transverse bar of chitin (text-figs. 6 & 7) marks the line of junction to the upper surface of the hypopharynx.

The difference existing between *Nemura* and *Chloëon* in respect of these organs appears therefore to be concerned merely with the degree of fusion of their adjacent surfaces.

Text-fig. 5.



Nemura sp. Tongue, dorso-lateral aspect. $\times 250$. *h.* Hypopharynx. *m.* Maxillula. *p.* Transverse sclerite at base of maxillula. *p.m.* Plate in ventral wall of maxillula.

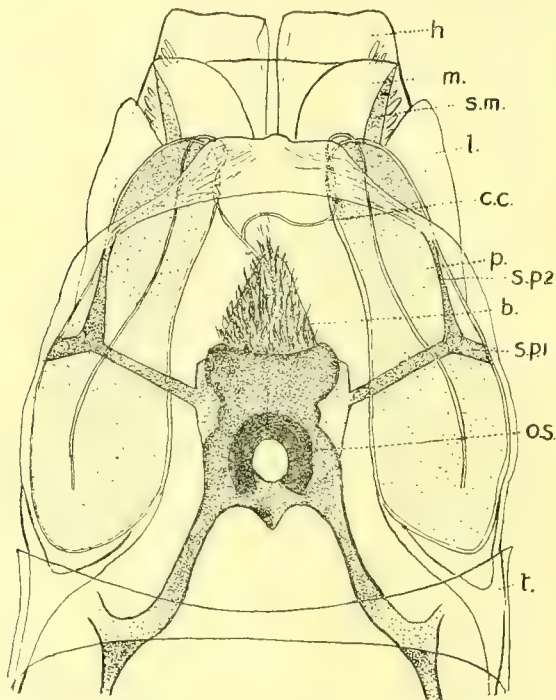
PSOCIDÆ AND MALLOPHAGA.

The tongue of Psocidæ (text-fig. 6) and Mallophaga bears a pair of oval, or sole-shaped, structures (*p.*) as to the nature of which considerable controversy exists. They were described by Burgess (5) in the Psocidæ and termed "lingual glands," but Burgess suggests that this term might not correctly express their nature. The chitinous cord (*c.c.*) proceeding from each, which unite, and pass backwards as a single cord, to be attached to the "bonnet-shaped" skeletal structure (*o.s.*), are referred to as "ducts" of these glands. Among later writers this interpretation has been followed by Snodgrass (43) and Shipley (41). The "glands" are, however, considered to be chitinous thickenings of the hypopharynx by Grosse (19), Mjoberg (34),

and Cummings (10). Enderlein (15) expressed the opinion that the "glands" are appendages homologous with the maxillulæ of Collembola, while Börner (4) calls them the "fulturæ" or lingual stalks, and says that the maxillæ are represented by a pair of membranous lobes attached to the tongue.

The mouth-parts of British Psocidæ are, owing to their minute size, exceedingly difficult of dissection, but, through the kindness of Dr. Imms,

Text-fig. 6.



Large Psocid. Tongue, dorsal aspect. The plates *m.* and chitinous cord *c.c.* are seen through the membranous dorsal surface of the hypopharynx and maxillula. $\times 250$. *b.* Brush-like sclerite. *c.c.* Chitinous cord = "duct." *h.* Hypopharynx. *l.* Lobe of hypopharynx. *m.* Maxillular lobe of hypopharynx. *p.* Chitinous plate = "lingual gland." *o.s.* Œsophageal sclerite. *s.m.* Sclerite rising from apex of plate (*p.*) and associated with *m.* *t.* Tendon.

I have been able to examine specimens of a very large species which is a native of India. The hypopharynx, whose walls are of very delicate membrane, is figured (text-fig. 6) from the dorsal surface. The ventral wall is thickened laterally to form the paired, convex, sole-shaped plates of yellow chitin (*p.*) (seen by transparency), the so-called "lingual glands." The size of the specimens made it possible to dissect out the hypopharynx and open up

the dorsal wall, so that there was no doubt at all as to the exact position of these plates. Chitinous sclerites (*s.p.1*) and (*s.p.2*) connect the outer edge of each with the upper surface of the hypopharynx. Distally arise sclerites (*s.m.*) reaching to the apices of the delicate lateral lobes (*m.*). These lobes bear the same relation to the hypopharynx as do the maxillæ of *Forficula*, and it seems highly probable, as Börner (4) suggested, that they represent these appendages in a somewhat modified condition. A pair of membranous lateral projections (*l.*) arises behind them and may possibly represent a basal lobe of the maxillulæ.

Attached to the base of each plate (*p.*) are the forks of a strong tendon (*t.*), whose presence strongly suggests that the chitinous structures associated with the hypopharynx are mechanical in function.

In order to settle the question whether or not gland tissue is to be found associated with the plates (*p.*), nymphal specimens of a small British species of the *Psocina* group were sectionized. The fixatives employed were Carnoy's fluid (cold) and Gilson's fluid (hot), and the sections were stained with Heidenhain's iron hæmatoxylin in some cases and Grenacher's hæmatoxylin and eosin. The tissue lying between the plates and the upper surface of the tongue was indistinguishable in structure from that seen in many parts of the other mouth appendages. In transverse sections through the tongue no histological difference could be detected between the median portion and that lying above the plates. This investigation, therefore, lends support to the assertion that these latter structures are not in any way glandular or associated with glands. They are to be looked upon as thickened parts of the ventral wall of the tongue, which may possibly have originated as lingual stalks, or as the basal portions of maxillulæ which have become incorporated into the hypopharyngeal wall.

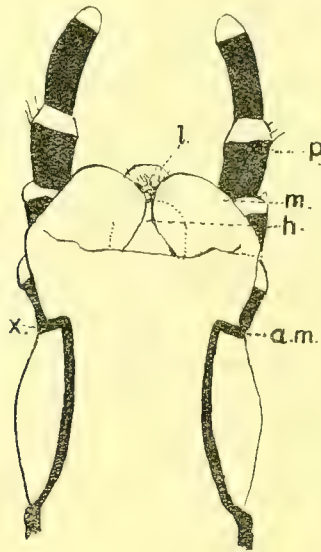
NEUROPTERA.

Raphidia.—Adult forms of a species of *Raphidia* were examined and in them the hypopharynx revealed some features of great interest. Text-fig. 7 (p. 440) represents the labium and floor of the mouth as seen when viewed from the dorsal surface; (*p.*) is the labial palp and (*l.*) the bifid, dorsally flexed, extremity of the single median endite borne by the mentum. See Westwood (46. pp. 45–56). The opening of the salivary duct occurs above the labium and ventral to the median fleshy projection (*h.*) in the floor of the mouth. This rounded lobe I regard as the hypopharynx or its distal portion. It is almost obscured by two others of similar membranous texture (*m.*). Each lateral lobe measures .14 mm. in length and .11 mm. in width. In texture and relative positions these three lobes bear a decided resemblance to the median hypopharynx and lateral maxillulæ of *Forficula*. Since the Neuroptera are amongst the less specialised Endopterygota it is possible that a true homology underlies this similarity.

In the larvæ of *Sialis* and *Chrysopa* the hypopharynx was not found to bear any distinct indications of maxillulæ.

Sialis.—The labium of the adult *Sialis* is described by Westwood (46. vol. ii. p. 50). He states that the true labium, "ligula," does not extend beyond the palpi but is "internally dilated." Packard (36. p. 73) describes the lingua of *Sialis*. It is, he says, short rounded and little developed. He notes the presence of sensory hairs at the edge similar to those borne by threads of the maxillary and labial palpi.

Text-fig. 7.



Raphidia sp. Tongue, dorsal aspect. $\times 90$. a.m. Chitinous bar arising from mentum.
h. Hypopharynx. l. Ligula. m. Maxillula. p. Labial palp.

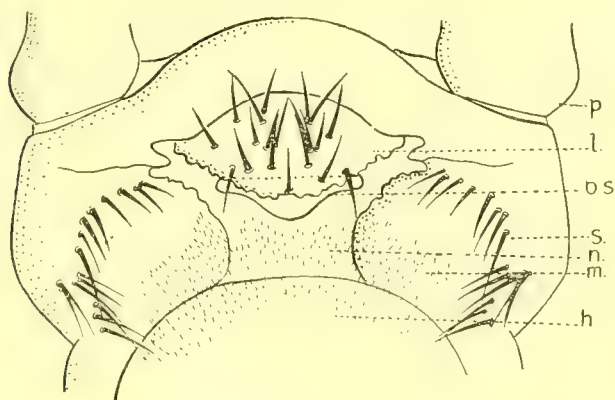
In text-fig. 8 (p. 441) this structure together with the hypopharynx (*h.*) is shown as viewed from before. (*l.*) is the anterior border of the labium (ligula). At each side the labium is connected internally to the palp (*p.*), with a large rounded lobe bearing small fine setæ and at the end a row of long stiff hairs: apparently those referred to by Packard. Viewed from the dorsal surface these lobes present much the same appearance as the similarly located structures in *Raphidia*. They may therefore be maxillulæ. This view as to their nature is based partly on the fact that here as in *Raphidia* their texture resembles that of the mouth-floor and differs from that of the "ligula,"

Hemerobius.—The appearance of the mouth-floor of an adult specimen of *Hemerobius* sp. as seen from the dorsal surface is illustrated in text-fig. 9 (p. 442). It is seen that from the membranous hypopharynx (*h*) arise a pair of lateral lobes (*m.*), the surface of which, like that of the hypopharynx, is covered with minute setæ (not shown in the figure). These lobes are, according to my interpretation, maxillulæ which have assumed a somewhat ventro-lateral position with regard to the hypopharynx.

Later a fresh specimen of *Chrysopa flava* was examined. The labium and hypopharynx resembled those of *Hemerobius* in general characters and also in their relative position. Prominent lateral plates were present at the sides of the hypopharynx, entirely clothed with long fine setæ. They could be reflected outwards to a considerable extent.

It was hoped that investigation of the hypopharynx in larval and adult Neuroptera might throw light on the origin of the condition in which it

Text-fig. 8.



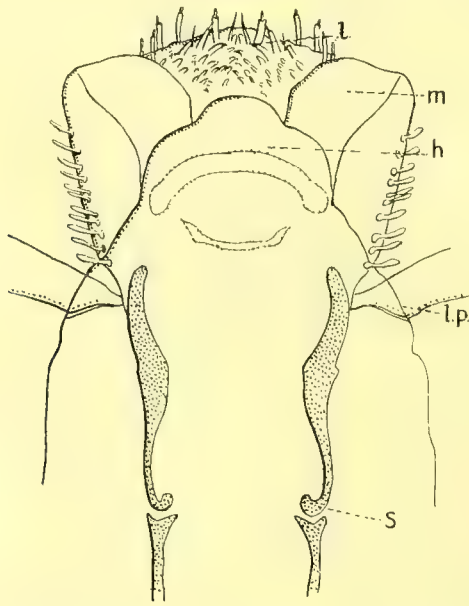
Sialis lutuaria. Labium and hypopharynx viewed from before. *h*. Hypopharynx. *l*. Ligula of labium. *m.* Maxillular lobe. *p*. Palp. *o.s.* Opening of salivary duct. *s*. Setæ bordering maxillula ventrally.

occurs in some of the mandibulate forms of Endopterygota. Now, let us suppose that the labium of *Forficula* were so reduced as to bear but a single median endite, and its sides fused with those of the tongue. The resulting structure would bear a distinct resemblance in constitution and appearance to the condition in *Raphidia*. These considerations suggest that in the latter such reduction and fusion have taken place. The maxillulæ in *Forficula* would, moreover, occupy precisely the same position with regard to hypopharynx and labium as do the lobes (*m.*) in *Raphidia*. It is therefore probable that these latter are wholly or partially the persistent maxillulæ.

In a later part of the present paper I have attempted to demonstrate a

close correspondence between the construction and arrangement of the hypopharynx and labium in a Tenthredian larva and that of *Sialis*. I have further suggested a possible mode of derivation of the condition in larval Lepidoptera and Trichoptera from one less specialised such as we found in larval Tenthredineæ. If there is any foundation for these suggestions then the Neuropterous types studied have afforded some clue to the mode of development of the highly specialised labio-hypopharyngeal structure of Lepidoptera from the free tongue and generalised labium of *Forficula*. They have, further, made it apparent that the possession of a pair of lobe-like projections is a feature of the hypopharynx in the Neuropterous forms studied. In dealing with the Tenthredineæ, reasons are given for assuming

Text-fig. 9.



Hemerobius sp. Labium and hypopharynx, dorsal aspect. *h.* Hypopharynx.
l. Dorsally flexed ligula. *l.p.* Labial palp. *m.* Maxillula. *s.* Sclerite supporting hypopharynx.

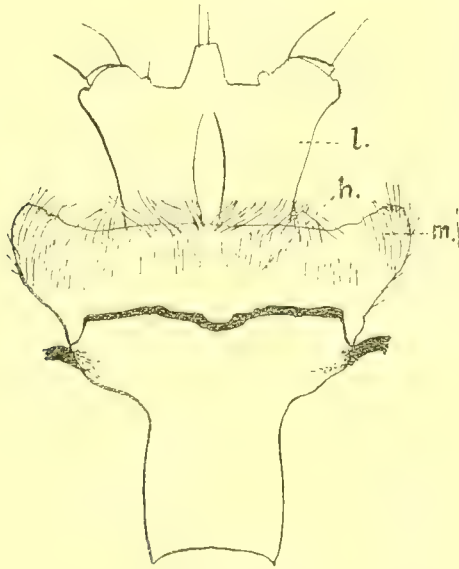
that the corresponding structures (*m.*) in that family are homologous with the maxillæ of Lepidopterous larvæ. I suggest, therefore, that in Neuroptera we find a condition of hypopharynx and maxillulæ intermediate between that of *Forficula* and larval Lepidoptera.

COLEOPTERA.

In the larva of *Helodes* Carpenter and McDowell (9. pp. 373-96) have described and figured a pair of articulated appendages, one at each side of the hypopharynx.

Homologous though reduced structures were found in *Dascillus*. These again were represented in a further reduced condition in the larva of the Lamellicorn *Geotrupes*. In a similar situation on the left side of the hypopharynx of the larval *Phyllopertha* occurred a very small lobe bearing teeth, a scarcely recognisable maxillula. In each of these cases it appears that the hypopharynx is membranous and is supported by a system of chitinous sclerites. It covers almost the whole of the surface of the labium to which it is fused or sutured in front. Of a totally different character is that of the larval *Pterostichus* described by Carpenter (7. p. 213, fig. 6). The anterior border is here broad transversely, set with long setæ and not united to the labium. Where this border comes into close proximity to the base of the maxilla it bears a small setose projection. This is regarded as a

Text-fig. 10.



Nebria brevicollis. Hypopharynx and labium, dorsal aspect. $\times 90$.
h. Hypopharynx. *l.* Labium. *m.* Maxillula (left).

maxillula, agreeing as it does in position with the process described by Magan (1912) in larval Dytiscidæ.

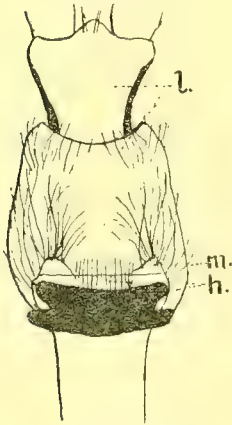
This latter type of hypopharynx I have found to occur in a modified form in larvæ of Staphylinidæ, Elateridæ, and the Malacoderm *Telephorus lituratus*. In other larvæ examined, Coccinellidæ, Tenebrionidæ, Chrysomelidæ, Cerambycidæ, and Curculionidæ, the structure was of the soft membranous character supported by sclerites. In the former group the labium extended considerably beyond the hypopharynx, and was not fused therewith anteriorly as was the case in the latter group.

In the Carabid, *Nebria brevicollis* (text-fig. 10), the larval hypopharynx (*h.*) is produced at the corners into two prominent lobes (*m.*) identical in position with the maxillulæ of *Pterostichus*. Apparently they are homologous with these appendages. Each measured $\cdot 09$ mm. in width, and the combined width of maxillulæ and hypopharynx was $\cdot 6$ mm. No distinct suture separating the maxillula from the hypopharynx could be detected. The maxillulæ here were more prominent than in the larvæ of *Pterostichus* and *Carabus violaceus* which were examined.

In various larval Elateridæ the hypopharynx was examined and great uniformity of construction was found to exist.

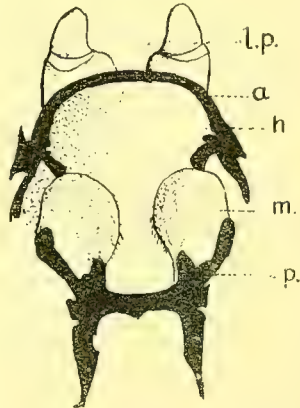
The condition seen in *Campylus linearis* will serve to illustrate the type. The hypopharynx (text-fig. 11), which is of stiff chitin, is supported by a

Text-fig. 11.



Campylus linearis. Labium and hypopharynx, dorsal aspect. $\times 90$. *h.* Hypopharynx. *l.* Labium. *m.* Maxillula.

Text-fig. 12.



Anatis ocellata. Labium and hypopharynx, dorsal aspect. $\times 55$. *a.* Anterior skeletal system. *h.* Hypopharynx. *l.p.* Labial palp. *m.* Maxillula. *p.* Posterior skeletal system.

stronger transverse chitinous plate. Its anterior border is independent of the underlying surface of the labium. It bears a pair of triangular plates (*m.*), measuring at the base $\cdot 05$ mm. These I regard as vestigial maxillulæ from considerations based on a comparison with those of *Pterostichus*. The combined width of the hypopharynx and maxillulæ is $\cdot 24$ mm. Each of the latter carries long, fine hairs which are mingled with similar but shorter hairs borne by the labium and by the basal portions of the maxillæ.

The larva of *Telephorus lituratus* is described by Miss O. M. Payne (38). From pl. 2. figs. 14, 15, in which the hypopharynx is shown, it seemed that this structure was very similar to that of Elateridæ. Examination of the mouth-parts of a specimen confirmed this supposition. I discovered hidden

by the long hairs which clothe the hypopharynx and labium a pair of very minute triangular projections situated at each side of the anterior border of the hypopharynx.

The similarity in character of the hypopharynx and maxillulæ and their relations with the labium in species of the Carabidæ, Dytiscidæ, Elateridæ, and Malacodermidæ gives support to the conclusions reached by Gahan (18) regarding the affinities of the Coleopteran families. This author states that the Adepnaga, including the Carabidæ and Dytiscidæ, is the most primitive group of the Coleoptera, and that the Malacoderms are a primitive family of the Polyphaga, and gave rise to the Elateridæ to which they are closely related.

I am indebted to Dr. Imms for specimens of the Coccinellid larva, *Anatis ocellata*. The hypopharynx (text-fig. 12) possesses a membranous, greatly convex, surface covered with minute spines. It is strengthened by an anterior (*a.*) and a posterior (*p.*) skeletal system. Supported in the angle between the two anterior arms of the latter arises on each side a rounded lobe (*m.*). Each measured .11 mm. in width, and the greatest width of the hypopharynx is .32 mm. These paired lobes may be compared in form (though they do not bear spines), and position upon the hypopharynx with the vestigial maxillulæ of *Geotrupes*.

A condition very similar to that last described was met with in the larva of *Doryphora decemlineata* where, however, the lobes were of much larger extent, practically covering the surface of the hypopharynx.

The hypopharynx in *Tenebrio mollitor* and *Otiorhynchus sulcatus* was found to possess indefinite paired dorsal lobes, which, however, could not with any certainty be looked upon as maxillulæ.

LEPIDOPTERA.

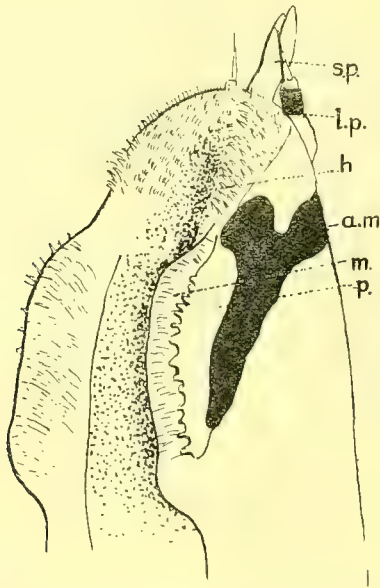
De Gryse (12, pp. 173-179) records the results of exhaustive investigations on the hypopharynx in a large number of Lepidopterous larvæ. On p. 174 he makes the generalisation that in larval Lepidoptera the maxillulæ "essentially present the appearance of protruding fleshy lobes, covering the floor of the buccal cavity wholly or in part only, These lobes are generally clothed with flexible lashes, with hairs or with rows of strong spines. In many instances the lobes are also furnished with chitinous blades" A feature common to the types described is the presence of a chitinous bar or "arm" arising from the mentum and at its distal end associated with the fleshy lobe.

I have examined the hypopharynx of a number of species of Lepidoptera belonging chiefly to the families Nymphalidæ, Pieridæ, Geometridæ, Noctuidæ, Lasiocampidæ, Pyralidæ, and Tineidæ. In most cases there was little that called for comment.

All the Noctuæ observed were found to agree remarkably closely with the condition found in *Mamestra persicariæ*. The right maxillula of *M. persicariæ* (text-fig. 13) measures $\cdot 51$ mm. in length from the point (*x*). From this level to the apex of the hypopharynx the distance is $\cdot 88$ mm. A thinly chitinised plate (*p.*) supports the outer wall of the maxillula to which it is closely applied. It is fringed with freely projecting teeth. The greatest width of the left lobe is $\cdot 2$ mm. The mental arm (*a.m.*) supports the chitinous plate for the greater part of its length.

The Rhopalocera investigated were not found to be strikingly different in the character of the hypopharynx from the Heterocera. In *Vanessa urticae*

Text-fig. 13.



Mamestra persicariæ. Labium and hypopharynx, dorso-lateral aspect. $\times 55$.
a.m. Mental arm. *h.* Hypopharynx. *lp.* Labial palp. *m.* Maxillula.
p. Plate supporting outer wall of maxillula. *sp.* Spinneret.

this structure was of a form commonly occurring amongst the latter group. This type, represented by *Lagoa crispata*, De Gryse (12. pl. 17. fig. 1), is found in both micro and macro-lepidoptera (p. 176). The fleshy lobes are "covered with spines but devoid of all traces of blades."

In *Pieris brassicæ* and *Philosamia cynthia* the maxillular lobes are very large in proportion to the hypopharynx; the proximal half of which they completely covered.

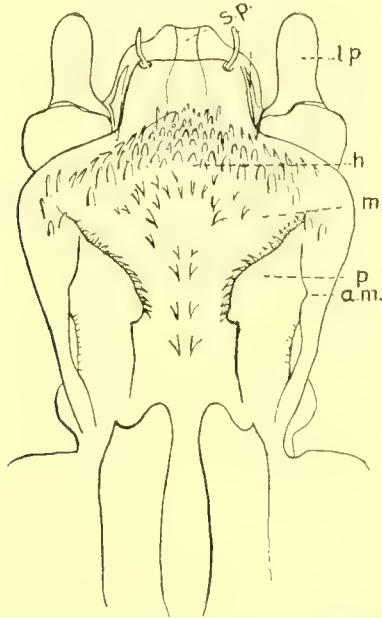
Considerable attention was devoted to examination of the condition of the

hypopharynx in *Hepialus humuli*. Although the family to which this species belongs is in many respects primitive the hypopharynx is apparently considerably specialised. It does not seem to afford any clue to the original form of the maxillulæ in Lepidopterous larvæ. The whole of the mouth-floor is remarkably soft, rounded and membranous, and the areas of chitinization very small. A pair of lateral membranous protuberances were too indefinite in character to be homologised with maxillulæ.

TRICHOPTERA.

The hypopharynx has been investigated in eruciform larvæ of *Phryganea* and Linnophilidæ and in the campodeiform *Rhyacophila* and *Hydropsyche*. It was found in most cases to bear a general resemblance to that of Lepidoptera. Its dorsal wall, forming the floor of the mouth, is produced distally to

Text-fig. 14.



Rhyacophila sp. Labium and hypopharynx, dorsal aspect. $\times 250$. *a.m.* Mental arm. *h.* Hypopharynx. *l.p.* Labial palp. *m.* Maxillular lobe. *p.* Plate supporting outer wall of lobe. *s.p.* Spinneret.

form a conical spinneret. Laterally its walls are continuous with those of the labium. With the exception of *Phryganea* all the examples investigated were found to be constructed on a common plan, which can be best described by a consideration of the condition in a species referable to the genus *Rhyacophila*.

The hypopharynx (text-fig. 14) measures .25 mm. in length and .22 mm. in greatest width in an almost fully-grown larva. In its median portion the upper surface is thrown into a pair of convex ill-defined lobes (*m.*) set with stout curved spines. Each is supported externally by a chitinous plate (*p.*) measuring .05 mm. in length and .03 mm. in breadth. The free edge of this plate is furnished with long hook-like spines. It arises from a chitinous lateral expanse (*a.m.*). This latter is seen to be continuous ventrally with the thickened portion of the mentum and is apparently homologous with the chitinous "arms of the mentum" in Lepidoptera. (In the larva of a Limophilid a narrow bar of chitin is found in this situation.) The condition of the mouth-floor in *Hydropsyche* sp. was similar to that of *Rhyacophila* sp.

It has been shown that paired lobes associated externally with chitinous plates occur in widely separated families of Trichoptera. This evidence seems to suggest that the possession of these structures is a feature characteristic of Trichopterous larvæ with certain exceptions. The hypopharynx, when these structures are present, is comparable in constitution to that of the more generalised Lepidoptera. In addition to the setiferous lateral lobes, it is characterised in both orders by (1) the possession of a conical spinneret, (2) the presence of chitinous arms extending from the mentum and associated dorsally with the exterior of the base of the lobes, and (3) the membranous rounded nature of the floor of the mouth. Thus the hypopharynx of Trichoptera is seen to be constructed on a plan fundamentally similar to that of Lepidoptera. The maxillulæ of the latter order are therefore in all probability represented in Trichoptera by the similarly located lobes (*m.*).

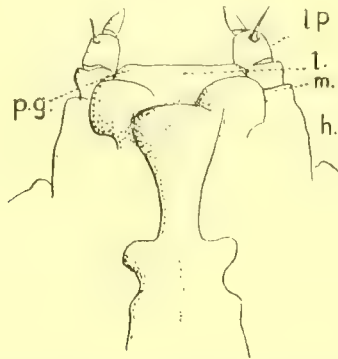
HYMENOPTERA TENTHREDINEÆ.

A vertical section through the head of *Hylotoma rosæ* Berlese (1. p. 522, fig. 595) shows that the duct of the labial or spinning gland runs above the labium to open above its extremity. Dorsal to the duct is seen a fold which constitutes the mouth-floor. The distal portion of this fold is, in all probability, the hypopharynx in Tenthredinian larvæ.

In a recent paper on the immature stages of the Tenthredinoidea McGillivray (31) fully describes and figures the mouth-parts of *Pamphilius dentatus*. It is stated that in *Pamphilius*, "On the dorsal surface of the ligula and laterad of the labial palpi, there is on each side a protuberance, a paraglossa. Between the labial palpi and arising on the ental surface, there is a prominent lobe which represents the glossa. The glossa has been modified into a spinneret (figs. 9, 13, sp.) for the opening of the duct of the silk glands." In fig. 13 the spinneret is seen as a structure projecting beyond the ventral surface of the ligula. It is therefore probably more highly developed than in the forms to be described.

This structure has been examined in various species, and considerable diversity was found to exist. Perhaps the simplest condition was that met with in *Selandria sivi*. The anterior portion of the labium (text-fig. 15) bears the three-jointed palps, and is scarcely differentiated into a median (*l.*) and two lateral portions (*p.g.*). The labium forms the ventral wall of a wide depression (*f.*) at the base of which is the end of the spinning duct. Dorsally this funnel is bounded by a rounded chitinous protuberance (*h.*), which is connected laterally with a similar pair of lobes (*m.*) closing in the sides of the funnel. They are the "glossa" and "paraglossæ" respectively of McGillivray (31). Each lateral lobe measures .18 mm. in length and .16 mm. in breadth. From their position in the floor of the mouth, and above the labial duct, I conclude that the median structure is the hypopharynx,

Text-fig. 15.



Selandria sivi. Labium and hypopharynx, dorsal aspect. $\times 55$. *h.* Hypopharynx. *l.* Ligula. *m.* Maxillula. *lp.* Labial palp. *p.g.* Paraglossæ.

and that the laterally associated pair may be maxillulæ or, at least, partly maxillular in constitution.

The mouth-parts of the larva of *Nematus Erichsonii* are typical of those of the majority of Tenthredineæ investigated. The surface of the hypopharynx and its dorso-lateral lobes is membranous and of rounded indefinite form.

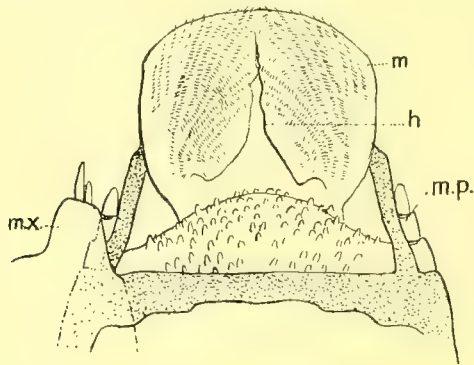
The larva of *Fenusa melanopoda* was found mining the leaves of alder-trees. When mature it measures 9 mm. in length. The internal structure of the head bears a striking resemblance to that of the young *Acroecrops* Heinrich and De Gryse (*loc. cit.* pl. 3. figs. 1 & 2). The mouth-parts are in both cases reduced and are associated with slender skeletal rods traversing the entire length of the head.

The mouth-floor of *Fenusa melanopoda*, viewed from above, presents the

appearance shown in text-fig. 16. Between the vestigial labial palpi (*m.p.*) projects the rectangular flat membranous structure (*h.*). Since this structure lies above the labial duct it is here considered to be the hypopharynx. It is supported laterally by two arms of the skeletal system. The length is .08 mm. and the greatest width .09 mm. The dorsal surface is markedly convex and bears two large convex plates (*m.*) covered with rows of minute spines. I regard these plates as maxillulæ, which have become flattened in accordance with the dorsi-ventral compression of the head.

A comparison between the anterior aspect of the labium and hypopharynx of *Sialis* and *Selandria* (text-figs. 8 & 15) reveals a close agreement with regard to the arrangements of the constituent elements. The salivary opening in both cases causes a slit-like depression above the border of the labium.

Text-fig. 16.



Fenusa melanopoda. Hypopharynx and maxillulæ, dorsal aspect. The maxilla is indicated on the left side only. $\times 400$. *h.* Hypopharynx. *m.p.* Labial palp. *m.* Maxillula. *m.x.* Maxilla.

Dorsal to it is a median lobe, the hypopharynx, whose lateral lobe-like expansions form the lateral walls of the depression. These latter are associated with the labium at each side behind the base of the palps. In *Sialis*, however, the ligula of the labium exists as a definite setose plate which is not represented in *Selandria*. This comparison points to the conclusion that the labium and hypopharynx of Neuroptera and larval Tenthredineæ are constructed on the same fundamental plan.

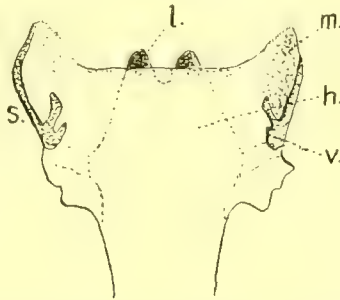
In discussing the labial gland of Tenthredinian larvæ, Berlese (1. p. 522) described its termination "sotto la lingua in una specie di filiera." This leads us to enquire how far the condition here may be compared with that of Lepidoptera.

We have noticed that the labium in larval Tenthredineæ is in a considerably reduced state, while in Lepidoptera it has become almost

unrecognisably modified to form the basal portion of the spinneret. Now in larval Trichoptera the spinneret is intermediate in development between that of Lepidoptera and the incipient condition of Tenthredineæ. It therefore appears likely that in the two orders in which a spinneret occurs it is derived from such raw materials as are afforded by the state of the hypopharynx and labium of Tenthredineæ. Assuming this to be the case, the hypopharynx of the latter order is homologous with the proximal portion of that of Lepidoptera. We should then expect that the simple lobes borne at the anterior lateral border of the hypopharynx in Tenthredineæ would be represented in a modified form in Lepidoptera, where they would occur at the sides of the hypopharynx behind the base of the spinneret. In this position we find the paired lobes considered by De Gryse as maxillulæ.

It, therefore, appears to me probable that the lateral lobes we have described in the mouth-floor of Tenthredinian larvæ are homologous with the maxillulæ of Lepidoptera.

Text-fig. 17.



Bibio pomonæ. Hypopharynx, dorsal aspect. The outline of the labium is indicated beneath the surface of the hypopharynx. *h.* Hypopharynx. *l.* Apical processes of labium. *m.* Maxillula. *s.* Sclerite supporting maxillula externally.

DIPTERA.

Bengtsson (2) announced the discovery of maxillæ associated with the endolabium in Tipulid *Phalaenocera*, stating that the latter structure was innervated by a pair of endolabial nerves arising from the sub-œsophageal ganglion dorsal to the mandibular nerves.

Traces of maxillulæ were sought for in the larvæ of various genera of Nemoceran diptera. These included *Chironomus*, *Tanytus*, *Bibio*, *Mycetophila*, *Tipula*, *Ptychoptera*, and *Simulium*. In the majority of cases the views of authors as to the exact limits of labium and hypopharynx were so various as to render impossible any definite conclusion as to the presence of maxillulæ associated with the latter.

In the case of *Chironomus*, however, we have the statement by Miall and Hammond (33. p. 29) that "The salivary ducts pass forwards to open above the mentum and behind a minute projection in the floor of the mouth (lingua)." When viewed from the dorsal surface the lingua (hypopharynx) of *Chironomus* sp. is seen to consist of a broad plate bearing at each side a wing-like projection which is inclined at right angles to the floor of the mouth. I have compared this condition with that found in two species of *Bibio*—*B. pomonae* and *B. Johannis*. Specimens of the latter species were kindly given me by Mr. H. M. Morris, M.Sc., and my description refers to *B. pomonae*. The only differences discovered between this species and *B. Johannis* with regard to the hypopharynx were those of size.

Morris (34 A. p. 96) describes the mouth-parts in his paper on the larval and pupal stages of this Nemoceran. I found that the salivary duct ran immediately dorsal to the thick bidentate structure, which is considered to be a portion of the labium. I therefore conclude that it represents the whole labium. In lateral view it appears not as a simple plate, but of composite nature. Above the end of the salivary duct is the membranous anterior portion of the mouth-floor. This has been described as the upper plate of the labium. Its position with regard to the labial duct appears to me to be conclusive evidence of the fact that it corresponds to the lingua or hypopharynx of *Chironomus*. Laterally it bears a pair of forwardly projecting pointed processes (text-fig. 17, *m.*) .2 mm. in length. These are so disposed that together with the hypopharynx they form a membranous crescentic structure. The exterior surface is supported by the arm of a chitinous sclerite *s.* The ventral portion (*v.*) of this sclerite is associated by means of a chitinous connective with the lateral angles of the labium.

The form of the hypopharynx and its lateral projections recalls in some features that of *Ilibius*, one of the less specialised Dytiscids, which belong to the most primitive suborder of Coleoptera. Moreover, Morris (1917, p. 104) gives reasons for regarding the larva of *Bibio* as primitive amongst Diptera. Thus, if maxillulæ exist in Dipterous larvæ, we should expect to find them present in such a form as this. The suggestion is therefore put forward that further investigation may demonstrate the maxillular nature of the processes borne by the hypopharynx in the larva of *Bibio*, and of the similarly located projections in *Chironomus*.

SUMMARY OF CONCLUSIONS.

Briefly, then, the presence of maxillulæ as a pair of appendages more or less closely associated with the hypopharynx is a characteristic feature of Apterygota. They are in the least modified condition in *Machilis*. I have emphasised the great degree of reduction which they present in *Lepisma*. They are well developed in *Forficula* though partially fused with the

hypopharynx. In the Ephemeroidea the maxillulæ lie between the mandibles and maxillæ, though they are articulated to the base of the hypopharynx. In larvæ of certain Perlaria Filopalpia I find structures projecting from the sides of the hypopharynx, which bear comparison with the maxillulæ of Ephemeroidea. In the section Setipalpia these appear to be represented by small setiferous convexities on the surface of the hypopharynx. My investigations do, I believe, tend to support the view that partially fused maxillulæ may be recognised in the membranous lobes associated with the hypopharynx in Psocidae and certain Mallophaga, and that the so-called "lingual glands" are chitinizations of the ventral wall of the hypopharynx.

In the Endopterygota the presence of maxillulæ is established in four families of Coleoptera. I have described structures which I regard as possibly homologous with these appendages in Elateridae, Staphylinidae, Telephoridae, Coccinellidae, and Tenebrionidae. Reference has been made to others of a more doubtful nature in *Doryphora* and *Otiorhynchus*.

The hypopharynx of Trichopteran larvæ bore comparison with that of Lepidoptera. On its dorsal surface were structures apparently homologous with the maxillulæ of Lepidoptera. Larvæ of *Sialis* and *Chrysopa* did not appear to possess these appendages. In the adults of species of these two genera of Neuroptera and in *Raphidia* the hypopharynx bore lateral structures which, from comparison with *Forficula*, seem to be wholly or partially maxillular in nature. Similarly located lobes, though modified in form, occur in larval Tenthredineæ.

Attention has been called to the presence of a pair of projections associated laterally with the hypopharynx of two Nemoceran Diptera, *Bibio* and *Chironomus*. It is doubtfully suggested that these are of the nature of maxillulæ.

A comparative review of the various conditions of the hypopharynx and maxillulæ of insects from the Apteriygota to the most highly specialised mandibulate Pterygota, points to the existence of a tendency to modification along certain lines, as follows:—

- (1) Greater association of the maxillulæ with the hypopharynx. (Compare *Lepisma* with *Machilis*, *Blatta*, and *Forficula*; *Perlodes* with *Nemura*).
- (2) Reduction in the size of the maxillulæ.
- (3) In Exopterygota the formation of a compound "tongue" composed of the hypopharynx and maxillulæ carried by a forwardly produced portion of the mouth-floor, specially developed for the purpose. This is seen in an incipient condition in *Chloëon* and *Nemura*. It is well formed in *Forficula*, Blattidae, and probably in Psocidae.

- (4) In the Endopterygota fusion of the distal portion of the mouth-floor with the labium. This occurs in the more specialised Coleoptera. Lateral fusion has taken place in the Neuropterous forms examined. The Tenthredinæ, Trichoptera, and Lepidoptera represent consecutive stages in the formation of a spinneret, by prolongation of the intimately fused labium and hypopharynx around the opening of the labial duct.

Finally, I wish to lay emphasis on the tentative character of the "conclusions" here reached. In certain of the orders and families considered maxillulæ were not hitherto known to be present. It is hoped that subsequent investigation into the embryological development and morphology of allied forms will reveal the truth with regard to this interesting question.

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EXPLANATION OF PLATE 31.

Petrobius sp. Dorsal aspect of Hypopharynx and Maxillulæ.
From a preparation stained with acid fuchsin.

a. Indication of articulation. *h.* Hypopharynx. *l.* Inner lobe of maxillula. *l₁.* Comb-like projection from surface of maxillula. *m.* Left maxillula. *p.* Palp. *p.e.* Peduncles of hypopharynx. *r.* Chitinous rods in ventral pharyngeal wall.



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